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ADDITIONAL OBSERVATIONS UPON THE STRUCTURE AND CLASSIFICATION OF THE MESOZOIC MAMMALIA.

BY HENRY FAIRFIELD OSBORN.

In connection with a visit to the recent Geological Congress in London the writer reviewed the British Museum collection of Mesozoic Mammals which formed the principal basis of a recently published Memoir[1] and examined also the valuable specimens at Oxford, Bath and York which had previously been studied merely from the descriptions and figures of Professor Owen and others. Also the *Neoplagiaulax* specimens in the collection of Dr. Lemoine at Rheims. There are two undescribed specimens in the Oxford Museum and since the writer worked upon the collection in the British Museum, (in 1886), many of the Purbeck fossils have been much more fully exposed by the further removal of the matrix. Important features have been brought to light, not visible previously, which lead to a revision of some of the conclusions which were reached upon the evidence then at hand. Greater familiarity with the minute Mesozoic types of molars sharpens the powers of observation and one is more apt to discover new points when on the lookout for them. Thus many inconspicuous but important features were noticed which formerly escaped attention. Some of these, such for example as the identity of *Amblotherium* and *Stylodon,* had been already anticipated, but others, such as the tritubercular molars of *Amphitherium* were entirely unexpected.

The following notes are in abstract from a Postscript to the Memoir, which is in preparation, and are not to be considered as final.

AMPHILESTES.

Besides Professor Owen's type, which is preserved in the York Museum,[2] there are two specimens belonging to this genus at Oxford. In the type, it is somewhat difficult to determine the number of the teeth, as described by Owen, since the incisor and canine alveoli are indistinct, but the Oxford specimens show that there were but *six* molars instead of seven as conjectured in Lydekker's Catalogue, Part V, p. 271, and adopted by myself, (op. cit., p. 193). In fact, one well preserved specimen, a right ramus seen upon the outer surface, shows but five molars. If this specimen be adult, as seems improbable, it may represent a new genus transitional between

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[1] "The Structure and Classification of the Mesozoic Mammalia." Journ. of the Acad. of Nat. Sciences of Philadelphia. vol. ix, no. 2, July 1888.

[2] I am indebted to Mr. Plattnauer, the Curator of this Museum, for the opportunity of freely examining this specimen.

Amphilestes with six molars and *Triconodon* with four. The second specimen, a left ramus also seen upon the outer surface, has three premolars *in situ* and the space for a fourth, (pm_1); in front of this is a deeper alveolus, probably for the canine, preceded by the alveoli of at least three incisors, so that the lower dental formula may now be given with considerable certainty as follows:

$$i.\ ?_3,\ c_1,\ p_4,\ m_6.$$

The canine is not preserved. The premolars as viewed upon the outer surface have prominent cingules but not the true basal cusps seen in *Triconodon.* The outer face of the molars is entirely devoid of a cingulum. None of the specimens give any evidence that the angle is distinct, but indicate that the lower border rises to the level of the condyle precisely as in *Phascolotherium*, *Spalacotherium* and *Triconodon.* This strengthens the writer's reference of these genera to one family as opposed to the views of Marsh and Lydekker; nevertheless, as shown below, *Spalacotherium* is a more specialized type than the others.

PHASCOLOTHERIUM.

Besides the type in the British Museum there is a beautifully preserved specimen belonging to this genus in the Oxford Museum and through the kindness of Mr. James Parker of Oxford the writer had an opportunity of examining a third specimen in his private collection. The latter, which has been figured in Phillips' "Geology of Oxford," is remarkable for the extension of the coronoid beyond the vertical line of the condyle. The Oxford Museum specimen[1] contains only the four posterior molars, probably m_4—m_7 with the fangs of m_2 and m_3. It may however be readily distinguished from the *Amphilestes* specimens by the stout cones and by the fact that the internal cingulum rises in two points upon the inner faces of the molars instead of in a single point beneath the protocone; also by the stout character of the jaw.

A renewed study of the molar teeth in the type specimen shows that all the post-canine teeth present the characters of molars in some respects. The *first* tooth behind the canine has a main cusp like that of the posterior molars and an internal cingulum horizontal and rising in two points instead of showing the sweep downwards and backwards which is so characteristic of premolar cingula. The accessory cusps are either covered with matrix or broken off. The *second* tooth has a fractured cingulum so that one cannot determine whether the anterior cusp is a cingule or a true paracone. The posterior cusp or metacone is prominent and distinct as in the premolars of *Triconodon*. The chief interest lies in the main cusp which is loftier and more pointed than the protocone of the *third* tooth which in turn has all the characteristics of a molar. This is an important point which has been overlooked previously, since it appears to indicate an available line of division in the functional adaptation of the series, *i. e.* a line between premolar and molariform teeth. If such a division be confirmed by further examination of the first and second teeth, it will lessen the gap between *Amphilestes* and this genus and remove what has been considered an entirely exceptional feature, viz. a type with no premolariform teeth. The mandibular formula may then be provisionally written thus: i_4, c_1, p_2, m_5.

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[1] The cast of this specimen in the Natural History Museum (M. 2300) has been mistakenly referred to *Amphilestes* by Lydekker, op. cit., p. 272, on the ground of "the small development of the accessory fore-and-aft cusps." The basal cusps of the molars are quite as prominent as in the type.

The crowns of this front pair of teeth have never been correctly represented. The writer's figure (op. cit., Pl. 8, fig. 3) is incorrect in restoring the cingulum of the second tooth and the basal cusps of the first tooth. In this Buckland's figure was followed, believing it probable that the jaw was in better condition when he figured it than now, for the last molar was then present. Another error in the drawing is the high position of the dental foramen, to which Professor Marsh kindly directed attention.

AMPHITYLUS.[1]

In the type of this genus at Oxford the teeth are so fractured that it is impossible to form any idea of their full structure. There is some doubt whether the dental formula, i_4, c_1, p_4, m_7, as generally given, is correct; one cannot be positive, for the 4th and 5th post-canine teeth are much mutilated; the characters of the condyle and angle, however, separate this specimen clearly from *Amphilestes*. At the time this genus was proposed the writer supposed we had in No. 36822 (Brit. Mus. Coll.) a ramus showing the outer face of the *Amphitherium* molars, but this proves to have been a mistake. The crowns of the last three molars in *Amphitylus* show a prominent posterior or third cusp, of which there is no evidence upon the molars of *Amphitherium*, as seen upon the inner face. The penultimate and ante-penultimate molars also retain this third cusp. The fourth, fifth and sixth molars counting from the last, show the trifid division of the crown characteristic of the triconodont type, then follow the two mutilated teeth with bifid crowns which may represent either premolars or molars. Thus the formula may read either

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[1] Proc. Acad. Nat. Sc. Phila. June 21, 1887.

i_4, c_1, p_5, m_6, or p_4, m_7, as given by Lydekker and adopted by the writer. Owen's formula, p_6, m_6, includes the canine in the premolar series.

PERAMUS.

We are fortunately able to greatly increase our knowledge of this genus. Upon uncovering the anterior molars of the type specimen of *Leptocladus*, an antero-internal cusp came into view, leading to the discovery that the latter genus is identical with *Peramus*, and still more interesting is the fact that the type specimen of *Spalacotherium minus*, (Owen) presents the much desired internal view of the *Peramus* molars. A third specimen confirms the facts derived from the second and shows that altogether there are six or, possibly, seven specimens in the British Museum collection which should be referred to this genus, giving us nearly all the characters of the mandibular dentition. These are:

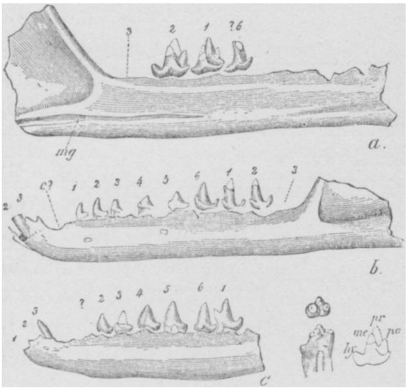

Fig. 1.

a. *Peramus* (*Spalacotherium*) *minus* Owen. Internal view of left mandibular ramus. *b.* *P.* (*Leptocladus*) *dubius* Owen. External view of left mandibular ramus. *c*, *P. tenuirostris* Owen. Outer face of anterior portion of left ramus. Also, Second Molar of *Amphitherium Prevostii* Owen, internal view. Also, Second molar of *P. minus*, enlarged from fig. 1 *a* above; internal view. *pr*, protoconid. *pa*, paraconid. *me*, metaconid. *hy*, hypoconid. *mg*, mylohyoid groove. Much enlarged.

The type, No. 47742, also No's, 47744, 47754, 47743. All except the last, portions of the left mandibular ramus seen upon the outer face. Referred by Owen to *Peramus* and so adopted by Lydekker (op. cit., p. 277.)

To which should be added:

No. 47,739, the type of *Leptocladus dubius*, (Owen, op. cit., p. 53, Pl. III, fig. 4; Osborn, op. cit., p. 239, Pl. 9, fig. 10; Lydekker, op. cit., p. 291.) A left mandibular ramus seen upon the outer surface.

No. 47,751, the type of *Spalacotherium minus*. (Owen, op. cit., p. 28, Pl. I, fig. 39.) A left ramus seen upon the inner face.[1]

The heel upon the molars of *S. minus* and the antero-internal cusp upon the antepenultimate molar of *Leptocladus* suggested a further examination which developed the fact that all the specimens of the above list agree in the following particulars: 1, In evidence of the presence of three incisors, (No's 47744, 47739, 47743). 2, In evidence, direct and indirect, of the presence of six *premolariform* teeth, (No's 47743, 47739, 47742). 3, In evidence of the presence of but three molariform teeth. 4, In the fact that the mylohyoid groove does not terminate at the dental canal but extends back beneath the lower border of the pterygoid fossa, (No's 47751, 47754). All the specimens which do not directly bear upon these four features of agreement support them indirectly, or at least present no negative evidence.

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[1] Also possibly, No. 47799, referred by Lydekker to *Spalacotherium minus*, op. cit., p. 294.

The formula, pm_6, m_3, is very exceptional, and Mr. Oldfield Thomas, who kindly examined these specimens and discussed the dentition with the writer, suggested a different division of the series. In No. 47739 the third and fourth premolars present lower crowns than the succeeding tooth, fig. 1 *b*, but this is apparently because the tips are not fully exposed. And as we have at present no other data than the mere form of the teeth, it seems that we are bound to take the dentition as it stands, exceptional as it is, and divide it provisionally as follows:

$$i_3,\ c_1,\ p_6,\ m_3.$$

The almost invariable presence of four premolars among the Mesozoic and recent mammals is a very difficult fact to explain. This genus and apparently *Amphitherium* are among the few exceptions. Why was the line drawn exactly to include five teeth behind the incisor series, the first of these developing into a canine?

In describing *Peramus* (op. cit., p. 263), the writer questioned the reference of the anterior portion of the jaw, (No. 47743) to it on several grounds, but now considers this less doubtful, as the single incisor preserved is very similar to that in No. 47744., and both differ from those of *Stylodon*, the only other type which this specimen resembles. The last premolar has a heel very similar to that of the molars. The molars, fig. 1 a, are very similar to those of some of the eocene Creodonta, presenting the primitive *tubercular-sectorial* type. Among the Jurassic Mammals, they apparently approach most closely the molars of *Amphitherium.*

AMPHITHERIUM.

A comparison of the three specimens belonging to this genus, two in the Oxford collection, and the one previously studied in the

British Museum, has enabled the writer to determine fully the structure of the molars and premolars and to correct a previous error.

In examining the first and second molars of the type specimen under a strong lens, an external cusp was detected directly between the internal pair, a discovery of great interest, since, in connection with the last genus, it adds two important types to the tritubercular series. This external cusp is probably the one referred to by Owen, (op. cit., p. 14) in describing the penultimate molar of the second specimen of *Amphitherium.*[1] He speaks of the latter tooth as the posterior molar, but one can detect the tips of a molar behind this, just breaking through the jaw.

The molar of *Amphitherium* is thus apparently similar to that of *Peramus* with the exception that the external cusp, in the type species at least, is less lofty. This observation led to a reëxamination of the jaw in the British Museum, No. 36822. This unquestionably belongs to *Amphitherium*, as previously determined, (Osborn, op. cit., p. 192, fig. 2.; Lydekker, op. cit., p. 374), but presents the inner face of the right ramus instead of the outer face of the left ramus as previously described. This is proved by the double internal cusps, by the cingulum upon the premolar, and by the faint mylohyoid groove, near the lower border, which was previously overlooked. The individual is much smaller and younger than the two Oxford types, which are nearly of the same size, and the tips of the para- and metacones are entirely unworn.[2]

In the Memoir, the formula of *Amphitherium* was doubtfully given as pm_4, m_6, (following Lydekker). An examination of the Oxford types shows that Prof. Owen was more nearly correct in putting it, pm_6, m_6. If we deduct the foremost bifanged tooth which he naturally reckoned with the premolar series, but which is probably the canine, we have c_1, pm_5, m_6. In the second Oxford specimen there are undoubted traces of three premolars in front of the two complete ones. In front of these, Prof. Owen describes sockets for a bifanged tooth, (the canine), and for four single incisor fangs.

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[1] "The posterior molar shows a middle internal and part of a larger external cusp." This observation shows the keenness of the observer, for the molar referred to is in a very fractured condition.

[2] The teeth in the Stonesfield Slate specimens are much more brittle than those in the Purbeck series, but it would be well to run the risk of injuring one of these molars to expose the external cone.

PERALESTES.

A reëxamination of the superior molars in the type maxilla of this genus reveals an inconspicuous but important feature in the crown which escaped Professor Owen's notice as well as the writer's. That is, the presence of a low transverse crest connecting the antero-internal and antero-external cusps. This puts the functional adaptation of the *Peralestes* molar in a different light from that described in the Memoir, since it shows that this molar is *subtrenchant.* A close examination of the anterior faces of these crests, moreover, yields some evidences of wear by the crown of an inferior molar. These crowns are placed somewhat obliquely, but when the jaw is tilted so that the teeth can be viewed directly upon end, they are seen to have a triangular section, with the base with its lesser cusps directed outwards, and the main cone directed inwards, precisely as in the primitive tritubercular crown. When viewed in this way, this pattern at once suggests that of the *Spalacotherium* lower molars, which consists of a triangle reversing the above, *i. e.* with the main cone external and the base internal. Mr. Lydekker was the first to reach this conclusion as to the probable identity of these two genera but upon different grounds,[1] and the writer has hitherto held quite an opposite opinion,[2] which is now withdrawn.

The premolar formula of *Peralestes* is somewhat uncertain and the molars agree in number and size with those of *Spalacotherium.* At present, however, the evidence for the union of these genera is hardly sufficient to justify more than the placing of *Peralestes* in brackets with the above genus.

STYLACODONTIDAE.

After all the systematic work which has been done upon the genera embraced in this family, there are none in greater confusion as to nomenclature. As the writer anticipated after examining Prof. Marsh's *Dryolestes*, (Am. Naturalist, March 1888, p. 234 and Memoir, p. 236.) the genera *Amblotherium* and *Achyrodon* prove upon further examination and exposure of the crowns to belong to the *Stylodon* type.

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[1] "The true molars (of *Peralestes*) agree so closely in structure with those of *Chrysochloris* that there is every probability that the specimen belongs to *Spalacotherium tricuspidens*" op. cit., p. 294: In the writer's opinion, the molars of *Chrysochloris* bear only a remote resemblance to those of *Spalacotherium.*

[2] "A review of Mr. Lydekker's Arrangement of the Mesozoic Mammalia." American Naturalist, March, 1888, p. 235, "The molars of this genus are widely different from those of *Spalacotherium* etc."

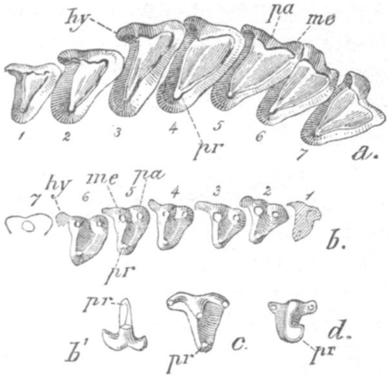

FIG 2.

a, *Kurtodon*. Superior molar series of the left maxilla, viewed upon the wearing surface. *b*, *Amblotherium soricinum*, inferior molar series, viewed from above. *b*1 *A.* (*Peraspalax*) *talpoides*. A lower molar viewed upon the internal face. *c*. The same. A lower molar viewed from above. *d*, *Achyrodon nanus*. A lower molar viewed from above. Much enlarged. Abbreviations as in fig. 1.

It further appears that Mr. Lydekker was correct in placing *Peraspalax* with *Amblotherium* (op. cit., p. 275), although he did not recognize the trituberculate character of the crown with the styloid external cone and two internal cusps and heel. The writer was in error, first in describing the external cusp of the molars of this genus (*Peraspalax*) as separated by a valley from the internal cusps, for there proves to be a distinct transverse crest; probably also, second, in associating this jaw with the *Peralestes* maxilla, (op. cit., p. 233).

It is now evident that the molars of Professor Owen's types of *Amblotherium soricinum* (Mes. Mamm., 1871 p. 29) of *A. mustelula* (ibid., p. 31.), of *Phascolestes longirostris* (ibid., p. 35.), of *Achyrodon nanus* (ibid., p. 37.), of *A. pusillus* (ibid., p. 39.), of *Peraspalax talpoides* (ibid., p. 40.), all present substantially the same crowns, (see Fig. 2). It is also probable, but not actually demonstrated, that *Stylodon pusillus* (Geol. Mag., 1866, p. 199.) and *S. robustus* (ibid.) have the same molar pattern. Professor Marsh has further applied a series of generic and specific names to the closely allied American genera. Altogether it will prove a difficult matter to clear up the synonomy of these numerous species and will require a close examination and revision of all the material available.

It is singular, in view of the probable similarity of many of these species, that all the specimens referred to *Stylodon*, because exposing the external face, possess but seven molars, with one possible exception, while three of the specimens shown upon the inner face have eight molars. As derived from a study of Professor Marsh's collection, the basis of distinction between these genera will depend: 1, upon the number of the teeth in the adult condition; 2, upon the presence of a heel, which is apparently wanting in *Asthenodon*; 3, upon the presence of one or of two transverse crests connecting the external with the pair of internal cones.

The name *Stylodon* is preoccupied, but *Amblotherium* has the precedence of *Stylacodon,* (Marsh) and *A. soricinum* can probably be retained for the larger species with seven molars, thus embracing *S. robustus* with which it agrees closely in measurement. *Phascolestes* would then embrace the species with eight molars. But these questions can only be finally determined by a careful revision of all the material.

It now seems probable that the type maxilla of *Kurtodon* (No. 47755.) fig. 2 *a*, should be placed somewhere in this series, as held by Owen and not represent a distinct family as maintained by the writer. Since the original study and figuring of the molars, the matrix has been extensively removed, so that the outer faces of the crowns are exposed and show a low antero-internal cusp near the base of the crown; this cusp is very important because it is apparently homologous with the postero-internal cusp of the *Amblotherium* lower molar. Further, as Mr. Lydekker has pointed out (op. cit., p. 291) the block No. 47786 (*S. pusillus?*) contains upper molars of a very similar pattern associated with lower teeth, resembling those of *Stylodon.* It is freely admitted that the views before expressed by the writer are not sustained by this additional evidence, although as to the more definite question, it is not as yet evident with which of these jaws the *Kurtodon* maxilla should be placed. The question will be settled by the exposure and study of the crowns of the numerous specimens referred to *Stylodon.* The *Kurtodon* crowns are unlike those of *Amblotherium soricinum* or of *Achyrodon* since the summit is much broader and the wearing surface, instead of being trenchant, is grinding, as previously described, (op. cit., p. 109).

SUMMARY.

The principle features of the present contribution are the following: 1, Additional characters of *Amphilestes* and the probable determination of the premolar-molar formula. 2, Additional characters of *Phascolotherium,* suggesting a division between molars and premolars. 3, A review of the *Amphitylus* dentition. 4, The union of *Leptocladus dubius* and *Spalacotherium minus* with *Peramus*, and determination of the mandibular dentition of the latter genus. The molars are tritubercular. 5, The discovery also of apparently tritubercular molars in *Amphitherium* and probable determination of the premolar-molar formula, (confirming Owen's views). 6, Confirming Lydekker's suggestion of the probable union of *Peralestes* with *Spalacotherium*, and of *Peraspalax* with *Amblotherium*. 7, The probable union of *Peraspalax, Amblotherium, Achyrodon, Phascolestes, Stylodon* and *Kurtodon*, into two or three genera with a substantially similar molar structure. 8, The correction of the writer's former views as to the family separation of the *Peralestidæ* and probably of the *Kurtodontidæ*.

The general result of the renewed and more extended study of these mammals has thus been, first to reduce the number of genera and eliminate two of the families proposed in the Memoir; second, by the discovery of the molar structure of *Amphitherium* and *Peramus*, to substantially reduce the number of molar types among the English genera to two, viz.: the *triconodont* in *Amphilestes, Phascolotherium, Triconodon* and probably *Amphitylus*, and the *tritubercular* in all the remaining genera.

This latter result is of great interest in its bearing upon the theory that the molar teeth of all the mammalia have either passed through the tritubercular stage or have been arrested at one of the steps in tooth development leading to this stage.